

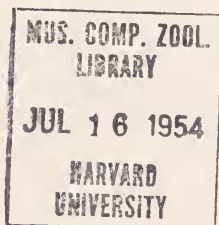
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**THE FOSSIL PIT-VIPERS
(REPTILIA: CROTALIDAE) OF NORTH AMERICA**

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INTRODUCTION

In 1920, Hay referred several fossil rattlesnake vertebrae to existent species. Later Gilmore (1938) could find no differences between the vertebrae of recent species of rattlesnakes, much less between the vertebrae of the various genera of the Crotalidae. He therefore referred all the fossil crotalids to *Crotalus* sp. except for the large vertebrae from the Pleistocene of Florida which, on the basis of size and distribution, he referred to the recent species, *Crotalus adamanteus*.

For several years the writer has been studying the comparative osteology of the rattlesnakes and their relatives and has found that not only the genera, but the species as well, can be distinguished on the basis of skull and vertebral characteristics. The results of this study will be presented elsewhere, with reasons for reaching certain conclusions as to identification of species (Brattstrom, MS.). During the study here reported the fossil crotalids in the various museums in the country have been examined. So that some of the names presented herein might be made available, this short summary of our current knowledge of the fossil rattlesnakes, copperheads, and moccasins of North America is presented.

The Crotalidae or "Pit-Vipers" are a family of solenoglyph or movable front-fanged, poisonous snakes showing remarkable parallel and convergent evolution with the Old World family of true vipers (Viperidae). The Crotalidae differ from the Viperidae in many characters, the most important of which is the heat-sensitive facial or loreal pit lying in a depression that accommodates this pit in the maxillary bone.

The Crotalidae include six genera (*Crotalus*, *Sistrurus*, *Agkistrodon*, *Lachesis*, *Bothrops*, and *Trimeresurus*), of which *Crotalus*, *Sistrurus*, and *Agkistrodon* are the Recent North American representatives. The extinct genera *Neurodromicus* Cope, 1873 (Miocene-Oligocene); *Helagras* Cope, 1883 (Paleocene); and *Coniophis* Marsh, 1892 (Upper Cretaceous) were assigned to the Crotalidae by Hay (1902). These genera, except *Coniophis*, were placed in the broad family Viperidae (considering the Crotalidae as a subfamily) by Williston (1925). Gilmore (1938) removed *Coniophis* and *Helagras* from the Crotalidae and placed them in *Incertae Sedis*, but retained *Neurodromicus* in the family. Vanzolini (1952) has recently shown, and the writer concurs, that *Neurodromicus* should be placed in the Boidae. The oldest known crotalids are *Crotalus viridis* and *Agkistrodon contortrix* from the ?Lower Pliocene of Driftwood Creek, Nebraska.

The writer has referred the skeletal remains of rattlesnakes from the asphalt pits and limestone caves of California to existing species (Brattstrom, 1953a, 1953b). One fossil from Potter Creek Cave, California, however, differed from recent species and was described as *Crotalus potterensis* (Brattstrom, 1953b). As other Pleistocene material containing rattlesnakes was examined, short papers were published on the herpetofauna of some of the sites. This included some material from Florida (Brattstrom, 1953c) and from Gypsum Cave, Nevada (Brattstrom, 1954). Many identifications were made on fossil material in the various museums and these are now reported. In addition, one new species and one new subspecies are described herein.

The large number of vertebrae of *Crotalus adamanteus* from many Pleistocene sites in Florida makes possible a statistical comparison with Recent material. Differences are indicated that show a gradient, or intergradation in time. This problem has faced others (Howard, 1946; Colbert and Hooijer, 1953) and they solved the problem by considering the Pleistocene form as a subspecies of the Recent form. Though many of the characteristics are obvious and qualitative, to demonstrate further the differences, the method of ratio of log-differences of a series of analogous measurements was used. This method was developed by Simpson (1941) and used to good purpose by Colbert and Hooijer (1953) in showing differences between Pleistocene and Recent subspecies of mammals from China. It has proven to be very useful in distinguishing closely related forms on the basis of vertebrae (Brattstrom, MS.).

SYSTEMATIC LIST

Agkistrodon contortrix (Linnaeus)

Nebraska, Driftwood Creek, Hitchcock County, ?Lower Pliocene.
A.M.N.H. 7182, 2 vertebrae; A.M.N.H. 7185, 29 vertebrae.

These 31 vertebrae, representing the first record of fossil copperheads, do not differ from vertebrae of Recent specimens.

Agkistrodon piscivorus (Lacépède)

Florida, Seminole, Pinellas County, Late Pleistocene. A.M.N.H. 7181, 4 vertebrae.

Florida, Melbourne, Brevard County, Late Pleistocene. M.C.Z. 2111, 10 vertebrae.

Florida, Crystal Springs, 28 miles N.E. of Tampa, Pasco County, M.C.Z. 2116, 3 vertebrae.

Crotalus adamanteus pleistofloridensis, new subspecies

TYPE: A.M.N.H. Department of Vertebrate Paleontology, number 6779 (one mid-thoracic vertebra).

LOCALITY AND AGE: Seminole, Pinellas County, Florida, Late Pleistocene.

DIAGNOSIS: A *Crotalus* differing from *C. a. adamanteus* in being larger and in having a higher neural spine, a longer hypapophysis, the parapophysis longer and bent laterally, and the process of prezygapophysis wider than the process of the postzygapophysis.

DESCRIPTION OF TYPE: The holotype has a tall neural spine and an elongate hypapophysis (Figure 2). Neural spine widest at the top, zygosphenes indented slightly at the middle, prezygapophysis turned up slightly. Centrum cup and ball slightly wider than high, lower part of the parapophysis (prepophysis) longer than wide, the hypapophysis elongate and flat in its posterior part, widest (anteroposteriorly) at its base. Neural canal a little higher than wide, zygantrum deep and narrow with the result that the posterior part of the postzygapophysis process is solid. Area of vertebra between the process of the pre- and postzygapophysis straight, not curved.

Comparative measurements of all known specimens of *C. adamanteus pleistofloridensis* are presented in Figure 1. Measurements in millimeters of the type (and paratype) are as follows: Height, 36.9 (35.2); width, 14.8 (15.8); length at centrum from ball to cup, 11.8 (12.8); height of neural spine, 12.1 (10.0); width of neural spine, 8.7 (9.0); height of centrum, 6.4 (6.8); width of centrum, 7.0 (7.5); width across prezygapophysis, 25.0+ (27.3); width across postzygapophysis, 24.2 (24.2+); width of prezygapophysis process, 4.5 (4.6); width of postzygapophysis process, 4.1 (4.0); length of hypapophysis, 18.8 (19.5); width of hypapophysis, 4.1 (4.3); height of zygosphenes from top of cup, 7.0 (7.0); width across zygosphenes, 10.2 (10.9); length of anterior parapophysis, 5.0 (5.6); width of anterior parapophysis 3.4 (3.4).

REFERRED MATERIAL: (All from the Pleistocene of Florida)
A.M.N.H. 7170, Paratype, Seminole, Pinellas County, 1 vertebra.

- A.M.N.H. 6776, Seminole, Pinellas County, many vertebrae.
 A.M.N.H. 6778, "Allen Cave," Lecanto, Citrus County, 6 vertebrae.
 A.M.N.H. 7514, Florida, locality unknown, 17 vertebrae.
 U.C. 28910, Seminole, Pinellas County, 2 vertebrae.
 U.S.N.M. 13678, 2 miles W. of Melbourne, Brevard County, 19 vertebrae.
 U.S.N.M. 13679, near Melbourne, Brevard County, 5 vertebrae.
 U.S.N.M. 13677, near Melbourne, Brevard County, 3 vertebrae.
 U.S.N.M. 11220, 2 miles W. of Melbourne, Brevard County, 3 vertebrae.
 U.S.N.M. 11333, N. side Canal, Vero Beach, St. Lucie County, 46 vertebrae (figured in Gilmore, 1938, pg. 74, Fig. 31).
 U.S.N.M. 11856, Melbourne, Brevard County, 12 vertebrae.
 U. Mich. 1009-1010, Seminole, Pinellas County, 2 vertebrae.
 M.C.Z. 2101, Melbourne, Brevard County, many vertebrae.
 M.C.Z. 2112-2113, Vero Beach, St. Lucie County, 23 vertebrae.
 F.G.S. V-471, Florida, locality unknown, 1 vertebra.
 F.G.S. V-472, Stratum, Vero Beach, St. Lucie County, 1 vertebra.
 F.G.S. V-2455, V-3472, V-2413, V-3492, V-1630, Stratum 3, Vero Beach, St. Lucie County, 10 vertebrae.

DISCUSSION:

C. a. pleistofloridensis is most closely related to the recent form *C. a. adamantens* Beauvois from which it differs in the characters presented in the diagnosis above, but especially in its large size. The subspecies *C. a. pleistofloridensis* is extinct though it is survived directly by *C. a. adamantens*. The extinct subspecies occurs in the many Pleistocene localities mentioned above and in association with an extinct, still larger species (described below).

Photographs of the type, paratype, and several series of *C. a. pleistofloridensis* are shown in Figure 2. A vertebra of this subspecies was figured in Gilmore (1938), as *C. adamantens*, (Fig. 31, pg. 74) from Vero Beach, Florida.

Crotalus atrox Baird and Girard

Nevada, Gypsum Cave, Late Pleistocene-Recent (8,000 to 10,000 years)
 C.I.T. 94 vertebrae.

Texas, Bulverde, Bexar County, Middle Pleistocene, U.S.N.M. 9223, 10 vertebrae, 1 dentary, 1 maxilla and fang, 15 ribs.

Crotalus atrox was first found as a fossil by Hay (1920), from Texas. A vertebra from this collection was figured by Hay (1920, pl. 10, Fig. 2.), upside down. It was also figured by Gilmore (1938, pg. 73, fig. 30). The length of the fang from Texas is 11.0 mm.

Crotalus giganteus, new species

TYPE: A.M.N.H. Department of Vertebrate Paleontology number 6772 (one vertebrae).

TYPE LOCALITY AND AGE: "Allen Cave," Lecanto, Citrus County, Florida, Pleistocene.

DIAGNOSIS: A large rattlesnake related to *C. adamantens* but differing from it in the large size of the vertebra, centrum, hypapophysis, and parapophysis, and in having the hypapophysis widest (anteroposteriorly) at its tip and not its base.

DESCRIPTION OF TYPE: A large vertebra measuring 41.2 mm. high, 17.7 mm. wide, and 13.3 mm. long at the centrum from cup to ball (Figure 2). Neural spine relatively wide, front of zygosphenes even with the anterior edge of neural spine. Top of the zygosphenes slanting ventrally. Centrum round, parapophysis almost as wide as long, width across prezygapophysis greater than width across postzygapophysis, process of prezygapophysis wider than process of postzygapophysis. Hypapophysis longer than height of neural spine and widely expanded at its tip. The tip of the left prezygapophysis is broken in the type. Measurements of the type (in millimeters) are as follows: height and width of neural spine, 13.7 and 11.4; height and width of centrum, 7.5 and 5.6; width across pre- and postzygapophyses 29.6 and 29.2; width of process of pre- and postzygapophysis, 5.9 and 5.1; length and width of hypapophysis, 22.9 and 5.0; height of zygosphenes above centrum cup, 7.9; width across zygosphenes, 11.5; length and width of anterior parapophyses, 6.9 and 5.2. **PARATYPE:** Besides the type there is a fragment of a vertebra (A.M.N.H. 7171) that is designated as the paratype. This fragment contains the left side of the vertebra and the centrum at its posterior end. This centrum is also round (height and width, 7.5 and 7.5 mm.).

DISCUSSION: The type and paratype are figured in Figure 2, and their measurements are compared with those of Recent *C. a. adamantus* and Pleistocene *C. a. pleistofloridensis* in Figure 1, on a Ratio of log-difference scale.

C. giganteus most closely resembles *C. a. pleistofloridensis*, from which it differs in its much larger size and in having the hypapophysis widest (anteroposteriorly) at its tip. *Crotalus giganteus* is found in association with (and thus probably co-existing with) *C. a. pleistofloridensis* and *Lampropeltis getulus* in "Allen Cave." Recent *C. a. adamantus* attains a maximum recorded size of 7 feet, 4 inches. Judging from the large size of *C. a. pleistofloridensis* and the much larger *C. giganteus* vertebrae, it is possible to speculate as to the maximum sizes of these forms. It is possible that *C. a. pleistofloridensis* attained a length of 9 or 10 feet, and 12 feet was probably the maximum length for *C. giganteus*. The width of *giganteus* was probably similar to that of the modern boa constrictor. The species is extinct.

Crotalus horridus Linnaeus

Arkansas, Conard Fissure, Pleistocene. A.M.N.H. 6404, many vertebrae and the posterior half of a lower jaw.

Georgia, Near Cartersville, Pleistocene, U.S.N.M. 4887, 53 vertebrae.

Maryland, Cavetown, Middle Pleistocene, U.S.N.M. 9157, 2 vertebrae.

Maryland, Cumberland Cave, Pleistocene, U.S.N.M. 13772, 11 vertebrae.

Massachusetts, ———, Pleistocene, A.M.N.H. many bones, Hecht, MS.

Pennsylvania, Carlisle Cave, Pleistocene-Recent, U.S.N.M. 102698, 4 vertebrae.

Tennessee, Big Pigeon River, near Newport, Cocke County, Pleistocene, U.S.N.M. 13686, 13 vertebrae.

The only previously known fossil timber rattlesnake was the *C. horridus* discussed by Hay (1920) from Cavetown, Maryland. The material

from Massachusetts will be discussed by Hecht (MS), though I have examined the material and approve its identification as *C. horridus*. All the fossil material falls within the variation demonstrated by *C. horridus*.

Crotalus cf. lepidus Kennicott

Arizona, San Pedro Valley, Cochise County, Early Pleistocene. C.I.T. (no number), 1 vertebra.

The one small vertebra from the Pliocene of Arizona is probably *C. lepidus*, as it agrees with it in all characters. The fossil is so fragmentary, however, that it can only tentatively be referred to this species.

Crotalus mitchelli (Cope)

Nevada, Gypsum Cave, Late Pleistocene-Recent (8,000-10,000 years), C.I.T. (no number), 55 vertebrae plus one entire skeleton.

Crotalus potterensis Brattstrom

California, Shasta County, Potter Creek Cave, Late Pleistocene, U.C. 3129, 2 vertebrae, a part of a pterygoid, fragments of ribs and three other fragments of bones.

No other material has come to light since the recent original description of this extinct species.

Crotalus scutulatus (Kennicott)

Mexico, Zumpango, México, Pleistocene. C.I.T. Locality 310, C.I.T. (no number), 2 vertebrae.

These two mid-thoracic vertebrae do not differ from recent specimens of this species.

Crotalus viridis (Rafinesque)

California, Rancho La Brea, Los Angeles County, Late Pleistocene, L.A.C.M. Pits A, B, 81, U.C. locality 2052, many vertebrae.

California, McKittrick Asphalt, Kern County, Late Pleistocene, U.C. 35114, 35122, 35123, 35124, 35125, 35126, 35127, 35128, 20 vertebrae.

California, Hawver Cave, El Dorado County, Late Pleistocene. U.C. (no number), 5 vertebrae.

Iowa, Andrews Stone Quarry, above Sioux City, Pleistocene. U.S.N.M. 13655, 7 vertebrae.

Nebraska, Driftwood Creek, Hitchcock County, ?Lower Pliocene. A.M.N.H. 1639, many vertebrae, 2 fangs (length 7.0 and 6.8 mm. long), A.M.N.H. 1638, 2 vertebrae, A.M.N.H. 1637, many vertebrae.

Nevada, Gypsum Cave, Late Pleistocene-Recent (8,000-10,000 years). C.I.T. (no number), 17 vertebrae.

The California material of this widespread rattlesnake has been discussed (Brattstrom, 1953a, 1953b) as was the Gypsum Cave fossils (1954). As comparative measurements of *C. viridis* were given previously, the summary of the measurements made on the Gypsum Cave, Nebraska, and Iowa material is presented herein (Table I). The material from all three of these sites averages slightly larger than those from Rancho La Brea, though the maximum measurements are not larger than for the La Brea material.

AGE (12BBCAPS)

In the following list the North American Crotalids are listed by the age from which they have been recorded. An asterisk indicates that the species or subspecies is extinct.

PLIOCENE

Agkistrodon contortrix
Crotalus viridis

PLEISTOCENE

Agkistrodon piscivorus
**Crotalus adamantus pleistofloridensis*
Crotalus atrox
**Crotalus giganteus*
Crotalus horridus
Crotalus cf. lepidus
Crotalus mitchelli
**Crotalus potterensis*
**Crotalus scutulatus*
Crotalus viridis

LOCALITIES

In the following list the North American Crotalids are listed as to the fossil localities from which they have been found.

ARIZONA

San Pedro Valley, Early Pleistocene
Crotalus cf. *lepidus*

ARKANSAS

Conard Fissure, Pleistocene
Crotalus horridus

CALIFORNIA

Rancho La Brea, Late Pleistocene
Crotalus viridis
Hawver Cave, Late Pleistocene
Crotalus viridis
McKittrick Asphalt, Late Pleistocene
Crotalus viridis
Potter Creek Cave, Late Pleistocene
Crotalus potterensis

FLORIDA

"Allen Cave," Lecanto, Pleistocene
Crotalus giganteus
Crotalus adamanteus pleistofloridensis
Melbourne, Late Pleistocene
Agkistrodon piscivorus
Crotalus adamanteus pleistofloridensis
Vero Beach, Late Pleistocene
Crotalus adamanteus pleistofloridensis
Seminole, Late Pleistocene
Agkistrodon piscivorus
Crotalus adamanteus pleistofloridensis
Crystal Springs, Late Pleistocene
Agkistrodon piscivorus
No Locality, Pleistocene
Crotalus adamanteus pleistofloridensis

GEORGIA

Cartersville, Pleistocene
Crotalus horridus

IOWA

Andrews Strong Quarry, Sioux City, Pleistocene
Crotalus viridis

MARYLAND

Cavetown, Pleistocene
Crotalus horridus
Cumberland Cave, Pleistocene
Crotalus horridus

MASSACHUSETTS

_____, Pleistocene, Hecht, MS.
Crotalus horridus

NEBRASKA

Driftwood Creek, ?Lower Pliocene
Agkistrodon contortrix
Crotalus viridis

NEVADA

Gypsum Cave, Late Pleistocene-Recent
Crotalus atrox
Crotalus mitchelli
Crotalus viridis

PENNSYLVANIA

Carlisle Cave, Pleistocene-Recent
Crotalus horridus

TENNESSEE

Big Pigeon River, Pleistocene
Crotalus horridus

TEXAS

Bulverde, Pleistocene
Crotalus atrox

MEXICO

Zumpango, Pleistocene
Crotalus scutulatus

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TABLE 1

SUMMARY OF MEASUREMENTS (IN TENTHS OF MM.)
OF FOSSIL *Crotalus viridis*

Measurement	Locality		
	Number of specimens, range (in parentheses), and average of measurements		
	IOWA	NEBRASKA	NEVADA
VERTEBRAE			
Height	1(138)	4(70-113)97	2(79-113)96
Width	7(45-54)49	12(33-63)49	2(49-74)62
Length at centrum	7(60)60	12(40-64)53	2(55-62)59
NEURAL SPINE			
Height	3(30-49)41	7(19-41)30	2(19-28)24
Width	3(38-47)56	7(24-47)38	2(43-46)45
PREZYGAPOPHYSES			
Width across	5(85-98)91	10(58-117)80	2(87-126)107
Width of process	1(20)	7(10-20)17	2(20-23)22
POSTZYGAPOPHYSES			
Width across	4(84-87)85	12(63-106)81	2(88-119)104
Width of process	1(20)	7(10-22)18	1(20)
CENTRUM			
Height	6(27-32)30	8(20-33)29	1(30)
Width	6(28-32)30	8(21-34)30	1(33)
ZYGOSPHENE			
Width across	5(37-40)39	7(27-48)41	1(50)
Height from centrum	5(25-30)28	7(19-30)28	1(29)
Width of process	5(10-20)20	7(10-21)18	1(20)

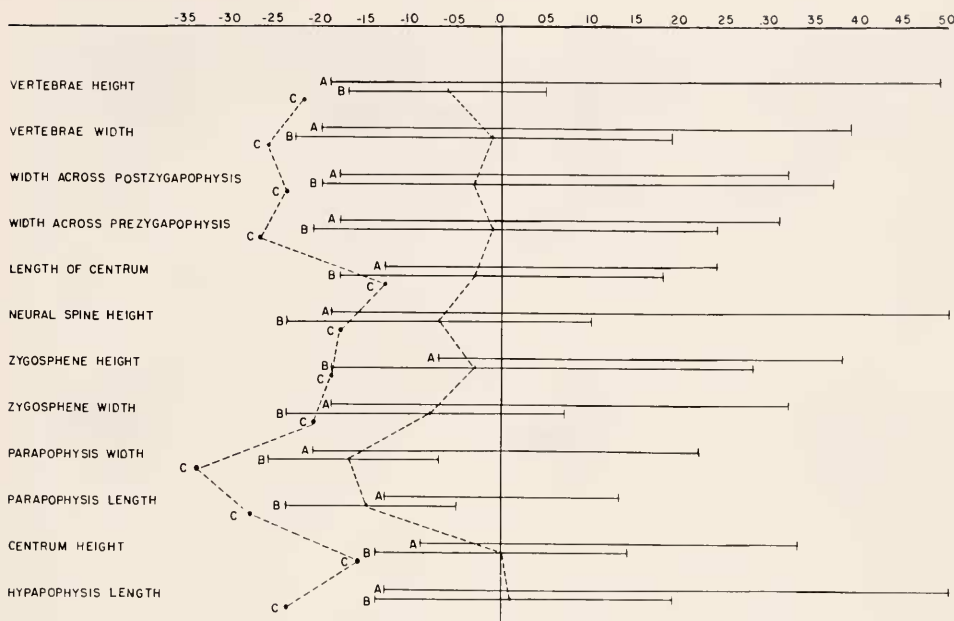


FIGURE 1. Ratio diagram (on a log-difference scale) showing comparison of certain osteological characters in *Crotalus giganteus* and two subspecies of *C. adamanteus*. A. Recent *C. a. adamanteus*, summary of many specimens. Standard (.0) is largest vertebra of a good-sized *C. a. adamanteus*, U.S.N.M. 29419. B. All Pleistocene material of *C. a. pleistofloridensis*; dashed line passes through average. C. Type of *C. giganteus*. A strong overlap is evident in A and B, with very little in C.



FIGURE 2. Thoracic vertebrae of *Crotalus adamanteus pleistofloridensis* and *C. giganteus*. 1 and 4, type and paratype of *C. a. pleistofloridensis*, Seminole, Florida. 5, 7, 8, 10, and 11, *C. a. pleistofloridensis*, part of syntypic series, Seminole, Florida. 6, 9, and 12, *C. a. pleistofloridensis*, A.M.N.H. 7514, Florida, no other data. 2 and 3, type and paratype of *C. giganteus*.